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An ecological study of the Collembola in a coniferous forest soil

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With 8 figures in the text

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Contents

1 Introduction

A survey of the literature on the soil Collembola showed that there had been no extensive work on their ecology in a single forest habitat and the aim of this work was to study the Collembola in the relatively uniform set of conditions provided by a coniferous forest. It was hoped to gain information on the horizontal and vertical distribution of the Collembola and the changes in their numbers over a period of time and to relate their distribution to environmental factors.

2 Methods

2.1 Choice of habitat

The habitat selected was a Douglas fir (*Pseudotsuga Douglasii* CARRIÈRE) plantation which had a complete canopy and no ground flora. The plantation was at Waen Wen, some three miles from Bangor, North Wales and has been adequately described by O'CONNOR (1957).

2.2 Method of extraction

The apparatus used for the extraction of the Collembola from the soil was based on the modified Tullgren funnel described by MACFADYEN (1953), but incorporated the 'split funnel' principle of P. W. MURPHY (1955). The samples were collected in stainless steel tubes ('corers') of approximately 5 cm. diameter and 4 cm depth. The undisturbed cores were inverted when placed in the extraction appartus so that the original upper surface was nearest the funnel and collecting tube (see MACFADYEN 1953).

It was not possible to test the efficiency of the apparatus directly, but the results obtained compare favourably with those of other workers (see MACFADYEN 1952 and MURPHY 1953).

2.3 Design of sampling

A sampling scheme was devised to cover twelve months, samples being taken at fortnightly intervals during this period. In order to study the vertical distribution of the Collembola it was decided to divide each core into litter, humus and soil sub-cores as the depths of the litter and humus in the soil profile were variable in the habitat selected. The capacity of the extraction apparatus allowed twelve complete cores to be extracted conveniently at one time (ie. thirty-six sub-cores).

As the trees in Waen Wen had been planted in parallel rows at approximately equal intervals each tree stood at the corner of a diamond-shaped area formed by the intersection of these rows. These diamond-shaped areas which had sides of approximately two metres and angles of 68° and 112°, were used as sampling units and will henceforth be referred to as 'squares' (see O'CONNOR 1957).

It was decided that the most representative method of sampling would be to take three random cores in each of four randomly selected squares; this would give some measure of both 'between-square' and 'within-square' variation.

A study area containing 520 squares was selected in the plantation and in order to give a good coverage of the area, it was divided into four plots of equal size (Plots A 1—4), from each of which one square was sampled at random once every fortnight (see O'CONNOR 1957).

A severe south-westerly gale on the night of November 29/30, 1954 brought down a large number of trees in the wood with the result that three-quarters of the study area had to be abandoned (Plots A 1, 2 and 3). In view of this, a second study area, adjacent to the first, was chosen (Study area B). This area was in most respects similar to the first, differing from it only in the texture of the mineral soil; this was crumbly and well-drained in Study area B in contrast with the compact soil of the original area. The same random sampling scheme was used for Study area B which was divided into plots (Plots B 1—4). To compare the two study areas, in each fortnight after the gale damage, one square was selected from the remaining plot (Plot A 4) of Study area A and three squares from Study area B (Plots B 1—3).

2.4 Collection and treatment of cores

The three layers of the profile were collected in separate corers. The litter sub-core was taken first, care being taken to cut the litter around the edge with scissors so that the corer could be eased in to prevent the compaction of the litter and the consequent death of some animals. This litter was then separated from the lower layers using a flat sheet of metal. The second corer was then pushed carefully into the humus, the depth of penetration being determined by examining the soil around the outside of the sample. Finally the mineral soil was sampled to a depth of approximately 3.75 cm. The ends of the corers were covered by a polythene sheet to prevent the escape of the more active Collembola and the drying out of the cores before they were placed on the extraction apparatus. Each sub-core was weighed before and after extraction and its depth recorded; in this way the dry weight and moisture content were obtained.

Variations in the depth of the humus within the diameter of the corer sometimes led to the accidental inclusion of some soil in the humus sub-core or vice versa, so that the separation of these layers could not be perfect.

2.5 Counting and identification of the Collembola

All Collembola in the year's samples were counted and identified, with the exception of ten specimens which were either damaged or poorly preserved. To determine the correct identification of the younger specimens of some species (eg. *Tomocerus minor* and *T. longicornis*) identified immature specimens were obtained from cultures. The identification of the Collembola was in accordance with GISIN (1944).

Table 1 shows the list of species found in Waen Wen plantation together with the numbers recorded during the year's sampling.

The data was analysed in detail for only the five commonest species of Collembola, ie. *Isotoma notabilis, Isotomurus plumosus, Friesea mirabilis, Tullbergia krausbaueri* and *Neelus minimus.*

Table 1. List of species occurring in Waen Wen study areas

Species	Numbers from the year's samples
Sub-order Arthropleona	
Tullbergia krausbaueri (BÖRNER)	5409
T. callipygos BÖRNER	487
Schaefferia willemi (BONET)	342
Friesia mirabilis (TULLBERG) f. *reducta*. STACH	3918
Anurida granaria (NICOLET)	59
Neanura muscorum (TEMPLETON)	63
Anurophorus laricis NICOLET	46
Folsomia quadrioculata (TULLBERG)	1028
Isotomiella minor (SCHÄFFER)	200
Isotoma notabilis SCHÄFFER	6985
I. olivacea var. *neglecta* SCHÄFFER	125
* *I. olivacea* var. *stachi* DENIS	5
I. viridis BOURLET	396
** *I. sensibilis* (TULLBERG)	—
Isotomurus plumosus BAGNALL	3387
Entomobrya sp.	17
Lepidocyrtus lanuginosus (GMELIN)	381
Tomocerus minor (LUBBOCK)	48
T. longicornis (MÜLLER)	41
Sub-order Symphypleona	
Neelus (Megalothorax) minimus WILLEM	2230
Sminthurides pumilis (KRAUSBAUER)	533
Sminthurinus aureus (LUBBOCK)	549
Sminthurus fuscus (LINNÉ)	14
Dicyrtoma minuta (O. FABRICIUS)	98
Unidentified (damaged or poorly preserved)	10
Total Collembola recorded	27359

3 Results

3.1 Abundance and Distribution

3.12 Collembolan aggregations

Examination of the figures for any of the fortnights' samples showed that, whereas most cores contained low numbers of Collembola, a few contained very large numbers. This suggests that the Collembola were aggregated and is confirmed for *I. notabilis* in Fig. 1 A which shows the frequency distribution of the cores for the first five sampling dates. This was obtained by calculating for each sample the number of cores in classes 0—1, 1—2, etc.

* These specimens could be described as *Spinisotoma stachi* DENIS.

** No specimens were found in the year's samples but one specimen was collected in a sample from the deeper mineral soil.

Note: the numbers of individuals recorded above represent those from an area of 0.586 sq. m., which is the total area covered by the year's samples.

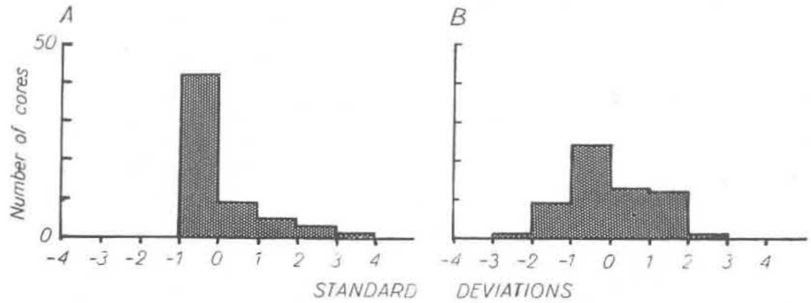


Fig. 1. The frequency distribution of the core totals of *I. notabilis* arranged about their sample means (fortnights 1—5). (A) Raw data. (B) Data expressed as log. (x + 1).

standard deviations away from the mean. The number of cores in each class were then summed to give totals for the five samples.

The range 0—1 standard deviations below the mean contains over two-thirds of the cores and this was offset by a small number of cores 2—4 standard deviations above the mean. This is a typical frequency distribution of an aggregated population, where most of the cores come from areas of low population but occasional cores come from areas of very high population.

The best statistical measure of aggregation is the variance: mean ratio or relative variance, which, in a random or Poisson distribution is equal to unity (CLAPHAM 1936) so that values greater than one indicate an aggregated population. The more aggregated the population, the higher is the relative variance. The statistical significance of the relative variance can be tested by the 't'test, where:

$$t = \frac{\text{difference}}{\text{standard error of difference}}$$

In this case the 'difference' is the departure of the observed value of the relative variance from that expected for a random distribution (ie. 'difference' = relative variance minus one). According to GREIG-SMITH (1952) the standard error of the difference is equal to $\sigma\sqrt{\frac{2}{(n-1)}}$, where n equals the number of cores.

The values for the relative variances for the five commonest species of Collembola in Waen Wen (see above) and for the collembolan totals (which include figures for all the collembolan species) are shown in Table 2. The variance estimate used in the calculation of the relative variance was the remainder variance after the between-plot variance had been removed together with the between-fortnight variance, thus eliminating the effects of large-scale patchiness and differences in the time of sampling.

Table 2. Values of the variance: mean ratios for five species of Collembola and the collembolan totals

	Study Area A	Study Area B
I. notabilis	21.47	38.24
Ir. plumosus	8.63	8.05
F. mirabilis	7.74	9.65
T. krausbaueri	20.75	41.48
N. minimus	14.03	7.47
Total Collembola	26.00	41.21

All the relative variance figures in Table 2 are significant at the 0.001 level of probability and the figures are high, indicating a high degree of aggregation. GREIG-SMITH (1952)

emphasises the importance of quadrat (or core) size in any study of aggregation. A core which is either too large or too small may give the impression of a random population and there is an optimum quadrat size for any population which can only be determined by taking quadrats of varying size. The relative variance figures therefore represent the minimum departure from a random distribution.

Isotomurus plumosus is the largest of the common species and has the consistently lowest relative variance; it is very probable, therefore, that aggregations of this species occupy a relatively large area and that the figures for relative variance underestimate the actual departure from random. It is therefore unprofitable to compare the relative variances of the different species as all are based on a single core size which may approach the optimum for some species but not for others.

The relative variance figures for total Collembola show a very aggregated population which suggests that two or more species have aggregations in the same places; if this were not so, the different species aggregations would tend to balance each other and this would result in a near random distribution. It is interesting to note that *I. notabilis* showed a much higher relative variance in Study area B than in Study area A, as also did *T. krausbaueri*. The reverse situation was the case in *N. minimus*.

3.12 Evidence of large-scale patchiness

Large-scale patchiness was estimated by comparing the between-square variance with residual variance and Table 3 shows the number of samples out of a total of sixteen for Study area A which have significant between-square variances.

These results show that in the majority of samples there was no greater variation between cores from different squares than between cores from the same square (ie. within a maximum distance of 2.5 m), and this shows that Study area A was uniform as a whole.

Table 3. The numbers of samples, out of sixteen from Study Area A, with significant between-square: residual variance ratios

	Level of probability (p).		
	0.05	0.01	0.001
I. notabilis	4	—	1
Ir. plumosus	2	1	—
F. mirabilis	—	1	1
T. krausbaueri	1	2	—
N. minimus	1	—	1
Collembola (all species)	1	—	—

3.13 Transformation of the collembolan data

For the purposes of statistical analysis, the core totals were converted into logarithms in order to obtain a symmetrical frequency distribution (see Fig. 1). QUENOUILLE (1950) states that a logarithmic transformation is appropriate where the standard deviation increases proportionately with the mean; Fig. 2 shows that this is true of the Waen Wen data for *I. notabilis*. The other four common species of Collembola and the collembolan totals were graphed in the same way and gave similar results.

3.14 Comparison of the two Study Areas

Although it was necessary (see 2.3) to change the study area during the year's sampling, one-quarter of the original area was retained (Plot A 4), and it is therefore possible to compare the two study areas. Since the population fluctuations over the whole year were to be considered this comparison was necessary. Two sets of analyses of variance were performed on each set of data, firstly on the data obtained previous to the gale damage (Plots

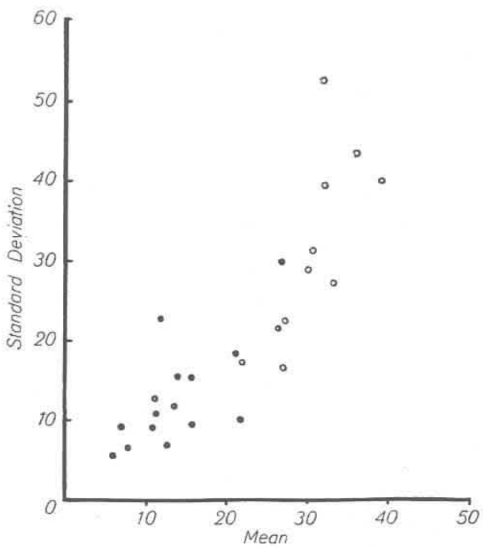


Fig. 2. Graph illustrating the relationship between the standard deviation (S. D.) of the samples and the sample mean for *I. notabilis*.
● Samples taken before the gale damage.
○ Samples taken after the gale damage.

A 1—4) and secondly on the data obtained after the gale damage (Plots A 4 and B 1—3). The analyses of variance were applied to the five common collembolan species, the moisture content, depth and weight of the organic layers and the moisture content of the soil.

In each of these analyses of variance the between-fortnight variance was eliminated and the between-plot variance: residual variance ratio was calculated. Where this ratio was significant a comparison of the means of the plots was made using the 't' test.

3.141 Study Area A (fortnights 1—16)

Neither the collembolan populations nor any physical factor showed a variance ratio significant at or above the 0.05 level of probability (see Table 4). Study area A can therefore be regarded as being homogenous and Plot A 4 is therefore typical of this area.

Table 4. Average numbers of Collembola in each plot and average values for physical data, expressed as core averages

	Fortnights 1—16 Plots				Fortnights 17—27 Plots			
	A 1	A 2	A 3	A 4	A 4	B 1	B 2	B 3
I. notabilis	16.6	14.3	15.2	12.4	5.75	22.8	38.4	20.1
Ir. plumosus	6.3	10.3	8.0	7.6	11.2	8.0	11.2	7.9
F. mirabilis	11.1	14.4	15.5	12.1	9.4	4.4	7.4	7.4
T. krausbaueri	17.5	19.0	18.8	24.6	10.0	4.9	4.5	13.3
N. minimus	11.0	9.7	17.0	8.8	6.9	3.6	4.8	5.3
Moisture content of:								
Litter	154	151	171	170	161	139	149	158
Soil	51	52	56	31	60	62	62	62
Litter + Humus	117	114	122	117	133	129	119	133
Depht of:								
Litter	1.30	1.30	1.34	1.25	1.47	1.48	1.50	1.96
Humus	1.56	1.21	1.60	1.45	1.68	1.53	1.44	1.61
Litter + Humus	2.86	2.51	2.94	2.70	3.16	3.01	2.94	3.60
Weight of:								
Litter	2.03	2.37	1.88	2.20	2.06	2.87	2.33	2.99
Humus	10.22	7.58	9.23	10.17	9.68	7.96	7.95	8.01
Litter + Humus	12.25	9.95	11.11	12.37	11.74	10.82	10.28	11.00

Moisture content: expressed as a percentage of the dry weight
Weight: measured in grammes
Depth: measured in centimetres

3.142 Study Area B and Plot A 4 (fortnights 17—27)

Study area B differed in two respects from Area A; firstly, there was much more variation between plots in Area B and, secondly, there was a much higher population of *I. notabilis* (see Tables 4, 5 and 6).

Table 5. Results of the analyses of variance on the data before and after the gale damage

Data	Plots A 1—4 (Samples 1—16) Between-Plot Variance Ratio	Degrees of Freedom N 1	Degrees of Freedom N 2	Plots A 4 and B 1—3 (Samples 17—27) Between-Plot Variance Ratio	Degrees of Freedom N 1	Degrees of Freedom N 2
1. Collembola						
I. notabilis	2.351	3	173	19.389***	3	118
Ir. plumosus	0.341	3	173	2.183	3	118
F. mirabilis	1.091	3	173	4.024**	3	118
T. krausbaueri	0.208	3	173	8.358***	3	118
N. minimus	2.398	3	173	1.077	3	118
2. Physical Factors:						
Moisture content of litter	2.126	3	160	2.621	3	118
Moisture content of soil	2.145	3	160	0.178	3	118
Moisture content of organic layer	0.371	3	160	1.265	3	118
Depth of litter	0.240	3	173	4.683**	3	118
Depth of humus	2.476	3	173	0.755	3	118
Depth of organic layer	1.737	3	173	2.267	3	118
Weight of litter	1.232	3	160	2.078	3	118
Weight of humus	1.485	3	160	0.900	3	118
Weight of organic layer	1.236	3	160	0.365	3	118

Levels of significance: * p = 0.05 ** p = 0.01 *** p = 0.001

Table 6. Results of comparison of Plot means for the Samples 17—27 in Study areas A and B

	Difference between Plot Means (levels of significance) A 4 B 1	A 4 B 2	A 4 B 3	B 1 B 2	B 1 B 3	B 2 B 3
1. Collembola:						
I. notabilis	0.001	0.001	0.001	—	—	—
F. mirabilis	—	—	—	—	—	—
T. krausbaueri	0.01	0.01	—	—	0.05	0.01
N. minimus	—	—	—	—	—	—
2. Physical Factors:						
Moisture content of litter	—	—	—	—	—	—
Depth of litter	—	—	0.05	—	0.05	0.05
Depth of organic layer	—	—	—	—	—	—

F. mirabilis had a low population in Plot B 1 and *T. krausbaueri* had a low population in plots B 1 and B 2 but had numbers in plot B 3 similar to those in area A.

Physical factors also varied more in Study area B; this is illustrated by plot B 3 which had a litter layer which was significantly deeper than that of the other plots.

In addition to these differences in the two areas there were differences in the species composition.

3.15 The relation between collembolan numbers and environmental factors

The relation between the numbers of Collembola and environmental factors was determined by calculating the correlation coefficients (see Table 7).

Where the Collembola were correlated with more than one factor or two factors were related, the partial correlation coefficient was calculated as this allows one factor to be correlated with another while a third is held constant (see Table 8).

3.151 Selection of samples

As only twelve observations were available for a single day's sample, it was decided to use three successive samples all taken in one month. The fortnights 3, 4 and 5 (May 27—June 22, 1954) were selected, giving thirty-six observations in all.

The only recorded factor which varied during this period was the sample moisture content, owing to heavy rainfall between May 27 and June 8. In order to make the three samples comparable in this respect the moisture content of each core was expressed as a percentage of the sample mean. The moisture content of the humus was regarded as being unimportant in most cases as it was not a good estimate of the moisture content of the organic layer, owing to the unavoidable inclusion of varying amounts of mineral soil and that of the litter was regarded as the best estimate. The results of the correlations on the five commonest species are shown in Tables 7 and 8.

Table 7. Correlation coefficients

Environmental factor	Numbers from	Values of correlation coefficient (r)				
		I. notabilis	*Ir. plumosus*	*F. mirabilis*	*T. kraus-baueri*	*N. minimus*
Organic layer depth	LHS	**0.37**	0.00	**0.42**	0.00	**0.37**
Organic layer weight	LHS	0.04	0.33	—0.05	—0.24	0.06
Litter depth	LHS	0.29	0.14	0.33	0.25	0.29
Litter depth	L	**0.42**	0.03	0.32	0.29	**0.59**
Humus depth	LHS	0.28	0.09	0.30	—0.16	0.28
Humus depth	H	0.27	0.12	**0.42**	—0.13	0.01
Litter weight	LHS	0.16	—0.13	0.31	0.27	0.32
Litter weight	L	0.33	0.01	0.29	0.26	**0.59**
Humus weight	LHS	0.01	**0.35**	—0.09	—0.28	0.02
Humus weight	H	0.23	0.31	0.13	—0.20	—0.13
Litter % water	LHS	0.30	0.13	**0.41**	**0.35**	0.25
Litter % water	L	**0.37**	—0.08	0.29	0.32	0.33
Humus % water	LHS	0.23	—0.22	0.26	0.15	0.21
Soil % water	LHS	0.00	—0.20	0.17	**0.51**	0.04
L	H	**0.37**	0.08	**0.38**	**0.38**	**0.38**
H	S	**0.46**	0.16	**0.50**	**0.59**	0.24
LHS	S	**0.43**	**0.35**	—	—	0.27

Key

L = Numbers of Collembola in litter sub-cores
H = Numbers of Collembola in humus sub-cores
S = Numbers of Collembola in soil sub-cores
LHS = Numbers of Collembola in core
% water = water content as a percentage of dry weight.

The values of the correlation coefficient ($n = 35$) were $0.01 < p < 0.05 = 0.35$, $0.001 < p < 0.01 = 0.45$, $p < 0.001 = 0.55$.

Table 8. Partial correlations

Species	Nos. from	Correlated with	Constant factor	Partial correlation coefficient
I. notabilis	LHS	Litter depth	Litter % water	0.23
	L	Litter depth	Litter % water	**0.37**
	H	Humus depth	Litter % water	0.23
	LHS	Litter % water	Litter depth	0.25
	L	Litter % water	Litter depth	0.30
	LHS	Humus depth	Litter depth	0.27
Ir. plumosus	LHS	Humus weight	Humus % water	0.28
	LHS	Humus weight	Litter % water	**0.38**
	LHS	Humus depth	Litter % water	0.06
	LHS	Humus % water	Humus weight	— **0.44**
F. mirabilis	LHS	Litter depth	Litter % water	0.26
	L	Litter depth	Litter % water	0.26
	LHS	Humus depth	Litter % water	0.25
	LHS	Litter % water	Litter depth	**0.35**
	LHS	Litter % water	Organic layer depth	0.32
	LHS	Organic layer depth	Litter % water	0.33
T. krausbaueri ...	L	Litter depth	Litter % water	0.23
	H	Humus depth	Litter % water	0.19
	LHS	Litter % water	Litter depth	0.30
	LHS	Humus depth	Litter % water	— 0.25
	LHS	Litter % water	Soil % water	0.33
N. minimus	L	Litter depth	Litter % water	**0.55**
	LHS	Litter depth	Litter % water	0.24
	LHS	Humus depth	Litter % water	0.23
	L	Litter % water	Litter depth	0.22
	LHS	Organic layer depth	Litter % water	0.32

Note: All symbols as in Table 7; significant values of the partial correlation coefficient agree with the values for the correlation coefficient given in Table 7.

Isotoma notabilis

The numbers of individuals in a core show a correlation with the depth of the organic layer and the numbers in the litter sub-core are correlated with the depth and moisture content of the litter. This species therefore prefers a deep wet litter layer and of the two, the partial correlations show that the depth of the litter is more important. This collembolan is not confined to the litter layer and it is, therefore, to be expected that its numbers should be related to the depth of the organic layer as a whole. The numbers in each layer of the profile are directly related to the numbers in the layer below.

Isotomurus plumosus

Although this species is weakly correlated with the weight of the humus and consequently with the organic layer as a whole, it has no significant direct correlation with any of the measured physical factors. The partial correlations show that *Ir. plumosus* is positively correlated with the weight of the humus if moisture content is held constant and it is even more significantly negatively correlated with the moisture content when the weight is held constant; the reason for this negative correlation with moisture content is unknown and difficult to interpret.

Friesea mirabilis

The numbers of *F. mirabilis* occurring in the profile are correlated with the depth of the organic layer and its moisture content; the numbers occurring in the humus are related to the depth of that layer.

Like *I. notabilis* this species prefers a deep organic layer and damp conditions; these two factors are weakly correlated (see Table 7) and in the case of this species the partial correlations show that moisture is the more important factor. The correlation with the depth of the humus is due to its correlation with moisture content. As in *I. notabilis* numbers in each layer of the profile are correlated with the numbers in the layer below.

Tullbergia krausbaueri

The only physical factor with which *T. krausbaueri* is correlated is the moisture content of the soil. AGRELL (1941) shows that this species is ill-adapted to withstand dry conditions and dies very rapidly if exposed to atmospheres of low relative humidity. *T. krausbaueri* is able to live in the mineral soil and in the event of drought this must be its last retreat; it is therefore understandable that the soil moisture content is of direct importance to it. The numbers in the three layers of the profile are again correlated with the adjacent layers.

Neelus minimus

The total numbers of this species are correlated with the depth of the organic layer and the numbers in the litter are related to the depth and weight of this layer. The partial correlations show that, as in the case of *I. notabilis*, the depth of the organic layer is more important than its moisture content and that this is also true of the litter. The numbers in the three layers of the profile are correlated as in the three previous species.

3.16 Inter-relationships of the physical factors

The correlations between the different physical factors are shown in Table 9. The only significant correlation coefficients are for the weight and moisture content of the humus which are negatively correlated and the depth and weight of the organic layer which are positively correlated.

Table 9. Correlation coefficients for physical factors

Factors correlated		Value of r
Litter depth	Humus depth	0.11
Litter weight	Humus weight	— 0.16
Litter depth	Litter % water	0.26
Litter weight	Litter % water	0.24
Humus depth	Humus % water	— 0.03
Humus weight	Humus % water	**— 0.43**
Humus weight	Litter % water	0.16
Litter depth	Humus % water	0.09
Litter % water	Humus % water	0.12
Humus % water	Soil % water	0.01
Litter % water	Soil % water	0.28
Litter % water	Humus depth	0.22
Litter % water	Humus weight	— 0.16
Organic layer % water	Soil % water	0.09
Organic layer depth	Litter % water	0.31
Organic layer depth	Organic layer weight	**0.57**

Note: Symbols used as in Table 7; significant values of the correlation coefficient as in Table 7.

It is interesting to note that there is no correlation between depth (or weight) of the litter and that of the humus; nor is there any correlation between the moisture contents of the litter, humus and soil in a profile.

The negative relation between the weight and moisture content of the humus is probably due to the amount of mineral soil inadvertently gathered with the humus (see 2.4) or to

the proportion of mineral matter in the humus. As the mineral particles have a higher density and hold less water than the humus, any increase in the proportion of mineral particles would result in an apparent decrease in the percentage moisture content of the humus.

3.17 *Inter-specific relationships*

The correlation coefficients and partial correlation coefficients between the different species of Collembola were calculated (see Table 10).

Table 10. Interspecific correlations and partial correlations

Collembolan species Correlations			Value of r
I. notabilis	*Ir. plumosus*		0.00
I. notabilis	*F. mirabilis*		**0.43**
I. notabilis	*T. krausbaueri*		0.25
I. notabilis	*N. minimus*		**0.35**
Ir. plumosus	*F. mirabilis*		— 0.26
Ir. plumosus	*T. krausbaueri*		— 0.10
Ir. plumosus	*N. minimus*		0.10
F. mirabilis	*T. krausbaueri*		**0.43**
F. mirabilis	*N. minimus*		**0.70**
T. krausbaueri	*N. minimus*		0.24
Partial correlations		Constant factor	
I. notabilis	*F. mirabilis*	Organic layer depth	0.33
I. notabilis	*F. mirabilis*	Litter depth	**0.37**
I. notabilis	*F. mirabilis*	Litter % water	**0.35**
Ir. plumosus	*F. mirabilis*	Humus % water	— 0.22
I. notabilis	*N. minimus*	Organic layer depth	0.24
F. mirabilis	*T. krausbaueri*	Litter % water	0.34
F. mirabilis	*N. minimus*	Organic layer depth	**0.64**
F. mirabilis	*N. minimus*	Litter % water	**0.67**
F. mirabilis	*N. minimus*	Organic layer depth and Litter % water	**0.63**

Note: Symbols used and significant values of 'r' as in Table 7.

It is to be expected that high populations of *I. notabilis*, *F. mirabilis* and *N. minimus* should be associated through their common correlation with the depth of the organic layer and this was confirmed by the results. *F. mirabilis* is correlated with *I. notabilis*, *N. minimus* and *T. krausbaueri*, whilst *Ir. plumosus* shows no correlation with the other species.

The partial correlations show that *I. notabilis* and *F. mirabilis* are related partly through their common correlation with the depth of the organic layer and *F. mirabilis* and *T. krausbaueri* through their common correlation with moisture content. The weak correlation between *I. notabilis* and *N. minimus* is due to their common relation to the depth of the organic layer. The highly significant correlation between *N. minimus* and *F. mirabilis* cannot be explained on the basis of the moisture content or depth of the organic layer or the combined effect of both these factors.

3.18 *Vertical distribution of the twenty-one species of Collembola occurring in the sampled profile*

The percentages occurring in the litter, humus and soil of the sampled populations of each of twenty-one species were calculated and are illustrated in Fig. 3. The seasonal variations in vertical distribution for the five commonest species and for the Collembola as a whole are shown in Fig. 4. The variations in the percentage of the populations in the mine-

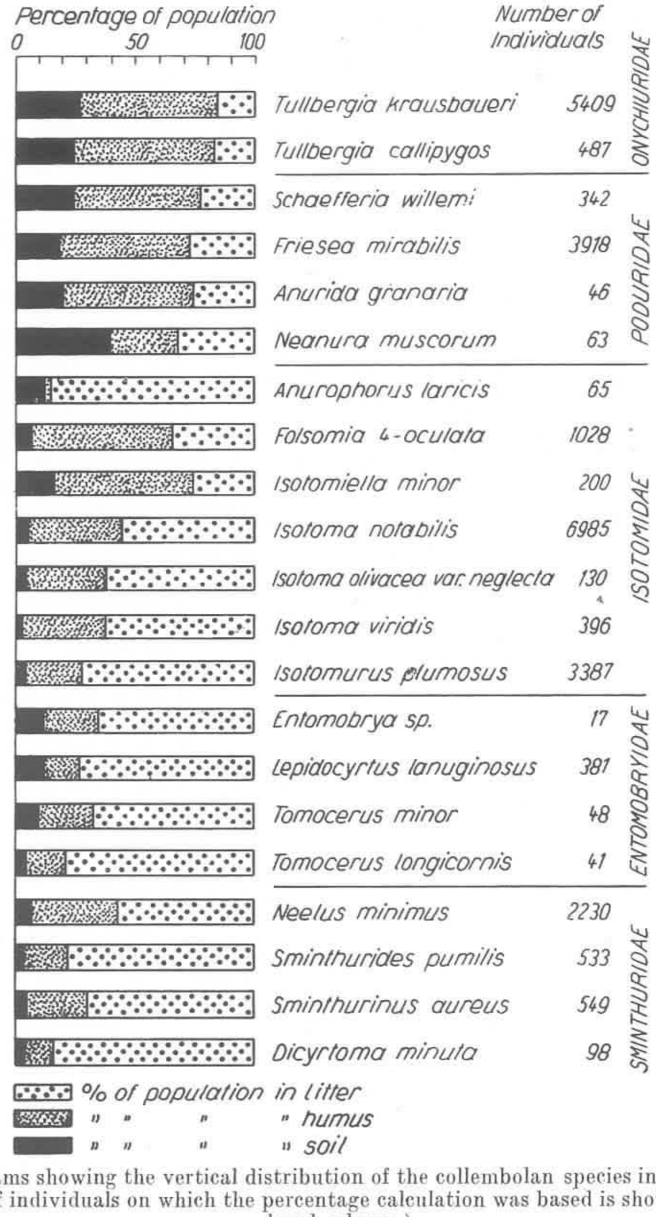


Fig. 3. Histograms showing the vertical distribution of the collembolan species in the soil profile. (The number of individuals on which the percentage calculation was based is shown in the right-hand column.)

ral soil will not be considered in detail owing to the sampling error caused by pockets of humus. The individual species are best considered together with other members of the same family.

Family Onychiuridae

This family has a smaller proportion of its numbers in the litter layer than any other family. The two representatives, *T. krausbaueri* and *T. callipygos* have an almost identical

distribution, their greatest numbers occurring in the humus. The vertical distribution of *T. krausbaueri* over the year remains very constant.

Family Poduridae

The members of this family, represented here by *Schaefferia willemi*, *Friesia mirabilis*, *Anurida granaria* and *Neanura muscorum*, like the Onychiuridae, are predominantly humus forms, but they tend to have larger numbers in the litter layer than the previous family. It should be noted that none of the Poduridae in Waen Wen possessed a functional spring. The vertical distribution of *F. mirabilis* shows little consistent variation during the year.

Family Isotomidae

There is a considerable range in both the morphology and vertical distribution of the members of this family. *Isotomiella minor* is a humus form with smaller numbers in the litter than any other member of this family. *Folsomia quadrioculata* is predominantly a humus form.

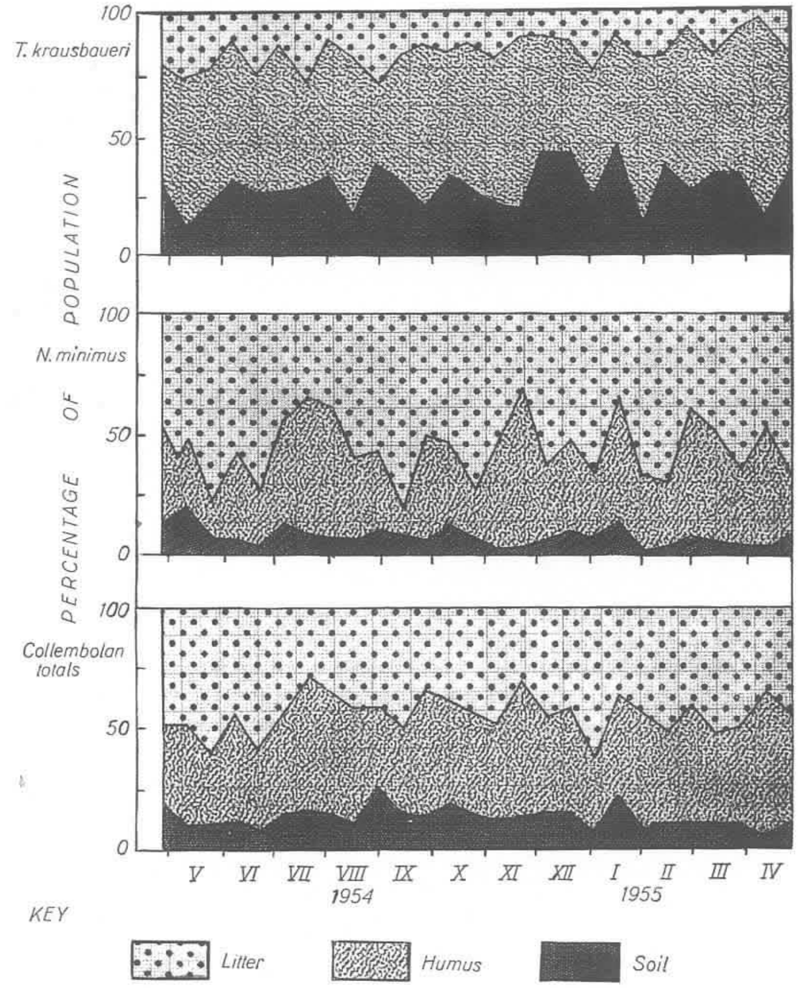


Abb. 4a

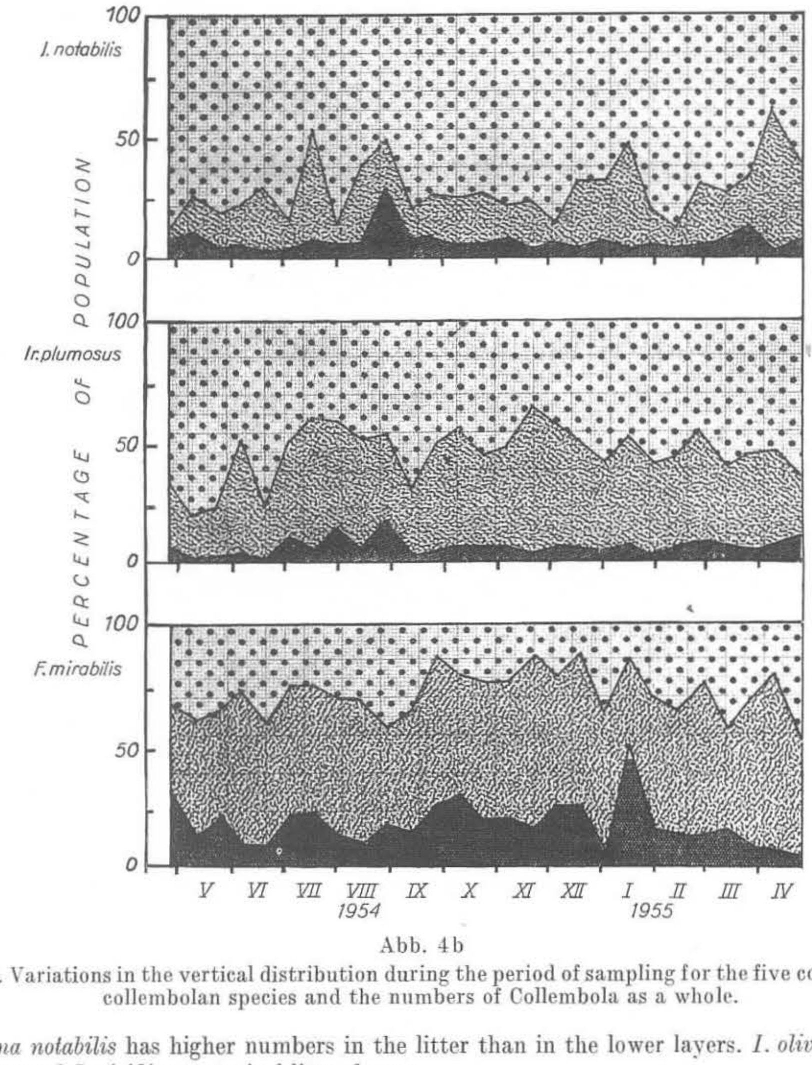


Abb. 4b

Fig. 4. Variations in the vertical distribution during the period of sampling for the five commonest collembolan species and the numbers of Collembola as a whole.

Isotoma notabilis has higher numbers in the litter than in the lower layers. *I. olivacea* var. *neglecta* and *I. viridis* are typical litter forms.

In this family, *Isotomurus plumosus* is the form most superficial in its distribution, over 70 % of the population occurring in the litter layer. The vertical distribution of *Anurophorus laricis* is peculiar but too much emphasis must not be placed on the results as they are only based on forty-six specimens; it is probably predominantly a litter form.

The vertical distribution over the year is considered for two members of the Isotomidae. *I. notabilis* starts with high litter populations in the spring followed by a decrease, reaching a minimum in July. This is followed by a slight increase which falls off to another minimum in November. *Ir. plumosus* shows minimum populations in the litter in August and late December 1954 and in April 1955.

Family Entomobryidae

The members of this family have been shown to live mostly in the superficial layers of the litter and amongst the surface vegetation (Agrell 1941, Axelson 1907), only immature

individuals being found in the humus. The results for *Lepidocyrtus lanuginosus*, *Tomocerus minor*, *T. longicornis* and *Entomobrya* sp. agree well with this.

Family Sminthuridae

The results for *Sminthurides pumilis*, *Sminthurinus aureus* and *Dicyrtoma minuta* con firm that the edaphic forms in this family are mainly found in the litter layer.

Family Neelidae

Neelus (*Megalothorax*) *minimus* occurs in considerable numbers in both litter and humus layers. During the year of sampling there were variations in the vertical distribution of this species, but there seems to have been a consistently low population in the litter during July.

3.19 Vertical distribution of the Collembola in the deeper mineral soil

In an investigation of the deeper distribution of the Collembola in the profile five cores were taken from the mineral soil in Study area A and five in Study area B. Each core was divided into sub-cores of 3.75 cm. depth. It was hoped that the cores would reach a total depth of 15 cm. but owing to stones and roots in the soil only five of the ten cores actually reached this depth.

Results:

Collembola were found in all sub-cores including the deepest where however, their numbers were small although the depth of penetration of the different species differed in the two areas (see Table 11).

Table 11. Species recorded in the study of the vertical distribution of Collembola in the mineral soil

Study Area A	Study Area B
B *Tullbergia krausbaueri* (e)	B *Tullbergia krausbaueri* (e)
—	A *Tullbergia callipygos* (e)
B *Schaefferia willemi* (e)	—
Friesea mirabilis (e)	B *Friesea mirabilis* (e)
—	B *Anurophorus laricis* (h)
—	A *Folsomia 4-oculata* (h)
Isotomiella minor (h)	B *Isotomiella minor* (h)
Isotoma notabilis (h)	B *Isotoma notabilis* (h)
Isotoma sensibilis (h)	—
Isotomurus plumosus (h)	—
Neelus minimus (h)	A *Neelus minimus* (h)
—	A *Sminthurinus aureus* (h)

Key to symbols
A specimens recorded below 3.75 cm. in the mineral soil
B specimens recorded below 7.50 cm. in the mineral soil
(h) hemi-edaphic forms
(e) eu-edaphic forms

In order to be certain whether a species can penetrate the mineral soil the first sub-core must be ignored because this contains the actual humus-soil interface and also frequently includes pockets of humus. Table 11 shows that the only species which occurred below the first sub-core in Study area A were *Tullbergia krausbaueri* and *Schaefferia willemi* both of which are well-adapted to a subterranean existence. In Study area B, however, all nine species found in the first sub-core also occur below 3.75 cm.; five of these species are even found below 7.5 cm. in the mineral soil.

This suggests that hemiedaphic forms are capable of penetrating the loose-textured soil of Study area B but are incapable of penetrating the compact soil of Study are A.

3.2 Species composition and seasonal variation

3.21 Species composition

Two aspects of the species composition were considered, firstly, the differences between the two study areas and, secondly, changes during the year of sampling.

Tables 13 and 14 show the species composition of the whole of the two study areas and of Plot A 4 both before (A 4a) and after (A 4b) the windfall. The species figures in Table 13 give the percentage species composition while those in Table 14 represent the average numbers of individuals per sample. All the average figures in Table 14 have been corrected to represent the same unit area. The figures for plot A 4 and for Study area B have been corrected to represent the area covered by one sample (ie. 0.0217 sq. m.), in order to be directly comparable with those of Study area A.

3.211 Comparison between Study areas A and B

The comparison of the species composition between the first and second study areas was facilitated by dividing the species into three classes 'abundant', 'numerous' and 'sparse' (see Table 12). This system was used for convenience and is not claimed to represent a natural grouping.

Table 12. Division of the species into three classes

Class Name	Numbers/sample	% of total Collembola (approximate)	Numbers/sq. m (approximate)
Abundant	over 50	over 5.0	over 2.300
Numerous	10—50	1.0—5.0	460—2.300
Sparse	under 10	under 1.0	under 460

Table 13. The percentage species composition of the different areas (only species which occur as more than 1 % of the population in any habitat are considered)

	Study Area A Samples 1—16	Plot A 4 (a) Samples 1—16	Plot A 4 (b) Samples 17—27	Study Area B Samples 17—27
Tullbergia krausbaueri	24.6	31.0	17.5	12.1
T. callipygos	2.3	2.2	2.1	—
Schaefferia willemi	1.6	1.1	3.4	—
Friesea mirabilis	16.3	15.2	16.3	10.3
Folsomia 4-oculata	2.1	2.1	6.8	5.8
Isotomiella minor	—	—	2.6	—
Isotoma notabilis	18.0	15.6	10.0	43.4
I. viridis	1.6	1.9	1.1	1.3
I. olivacea	—	—	2.4	—
Isotomurus plumosus	9.9	9.5	19.5	14.5
Lepidocyrtus lanuginosus ..	1.9	2.2	1.6	—
Sminthurides pumilis	2.6	2.7	1.6	—
Sminthurinus aureus	2.2	2.3	1.6	1.8
Neelus minimus	14.3	11.0	12.0	7.3

Plot A 4a is typical of Study area A as it has the same five 'abundant' species arranged in the same order, the 'numerous' species are the same in both cases and the figures for each species differ very little.

A comparison of plot A 4b with Study area B shows that *I. notabilis* is much more common in the latter, comprising 43 % of the collembolan population as against 10 % in Study

Table 14. Numerical species composition (average numbers per sample)

Species in numerical order Study Area A	Fort-nights 1—16	Plot A 4	Fort-nights 1—16
Abundant		Abundant	
1. *T. krausbaueri*	239.9	1. *T. krausbaueri*	295.8
2. *I. notabilis*	175.3	2. *I. notabilis*	149.0
3. *F. mirabilis*	159.2	3. *F. mirabilis*	145.0
4. *N. minimus*	139.4	4. *N. minimus*	105.3
5. *Ir. plumosus*	96.7	5. *Ir. plumosus*	91.5
Numerous		Numerous	
6. *Sminthurides pumilis*	25.5	6. *S. pumilis*	25.5
7. *Tullbergia callipygos*	22.3	7. *S. aureus*	22.0
8. *Sminthurinus aureus*	21.6	8. *T. callipygos*	20.8
9. *Folsomia 4-oculata*	20.3	*L. lanuginosus*	20.8
10. *Lepidocyrtus lanuginosus*	18.1	10. *F. 4-oculata*	20.0
11. *Schaefferia willemi*	15.4	11. *I. viridis*	18.3
Isotoma viridis	15.4	12. *S. willemi*	10.8
Sparse		Sparse	
13. *Isotomiella minor*	7.0	13. *T. longicornis*	5.3
14. *Dicyrtoma minuta*	4.3	14. *T. minor*	4.8
15. *Anurida granaria*	3.1	15. *I. minor*	3.8
16. *Neanura muscorum*	2.4	16. *D. minuta*	3.5
Tomocerus longicornis	2.4	*A. laricis*	3.5
18. *Tomocerus minor*	2.1	18. *A. granaria*	3.0
Isotoma olivacea	2.1	*I. olivacea*	3.0
20. *Anurophorus laricis*	1.6	20. *Entomobrya* sp.	1.0
21. *Entomobrya* sp.	1.0	21. *N. muscorum*	0.5
22. *Sminthurus fuscus*	0.8		
Unidentified	0.6		
Total Collembola	976.5	Total Collembola	953.2

area A (see 3.14). Apart from this species the order of abundance of the 'abundant' group was the same. Study area A had 8 'numerous' species whereas Study area B had only two, so that, although the species present are the same in both areas, the structure of the collembolan community differs in the two areas whose centres are only 100 m. apart.

3.212 Changes in species composition during the year

A comparison of the figures for plot A 4 before and after the gale damage shows that after the gale damage the following species were more numerous: *Folsomia 4-oculata*, *Isotomurus plumosus*, *Schaefferia willemi*, *Isotomiella minor* and *Isotoma olivacea*. There is also a slight increase in the total collembolan figures.

Only two species decreased after December 1954 and these were *Tomocerus longicornis* and *Tullbergia krausbaueri*.

The proportions of the five common species for the first and last months of sampling this plot (see Fig. 5) confirm the increase of *Ir. plumosus* and the decrease of *Tullbergia krausbaueri*. The small numbers of the other species do not justify their consideration.

3.22 Seasonal variations in environmental factors

Rainfall:

Weekly measurements of the rainfall were obtained and these were summed for fortnightly periods (see Fig. 6). They show that the year of sampling was exceptionally wet, the rainfall during the period being 52.9 inches (134.4 cm.) ten inches (25.4 cm.) higher than the average.

Table 14 (continued).

Species in numerical order Plot A 4	Fort-nights 17—27	Study Area B	Fort-nights 17—27
Abundant		Abundant	
1. *Ir. plumosus*	195.3	1. *I. notabilis*	473.2
2. *T. krausbaueri*	175.3	2. *Ir. plumosus*	157.9
3. *F. mirabilis*	163.3	3. *T. krausbaueri*	132.0
4. *N. minimus*	120.4	4. *F. mirabilis*	111.8
5. *I. notabilis*	100.4	5. *N. minimus*	79.6
6. *F. 4-oculata*	67.6	6. *F. 4-oculata*	62.8
Numerous		Numerous	
7. *S. willemi*	33.8	7. *S. aureus*	19.5
8. *I. minor*	26.2	8. *I. viridis*	14.4
9. *I. olivacea*	24.4		
10. *T. callipygos*	21.1	Sparse	
11. *S. pumilis*	16.4	9. *S. pumilis*	9.8
12. *L. lanuginosus*	16.0	10. *T. callipygos*	8.8
13. *S. aureus*	15.6	11. *L. lanuginosus*	5.8
14. *I. viridis*	10.9	12. *I. olivacea*	3.6
		13. *D. minuta*	3.5
Sparse		14. *N. muscorum*	2.1
15. *T. minor*	4.4	15. *I. minor*	1.9
16. *A. laricis*	4.0	16. *A. laricis*	1.2
17. *A. granaria*	2.9	17. *S. willemi*	0.2
N. muscorum	2.9	*T. minor*	0.2
19. *D. minuta*	0.4	*T. longicornis*	0.2
S. fuscus	0.4	20. *A. granaria*	0.1
T. longicornis	0.4	*S. fuscus*	0.1
Entomobrya sp.	0.4		
Total Collembola	1001.5	Total Collembola	1089.3

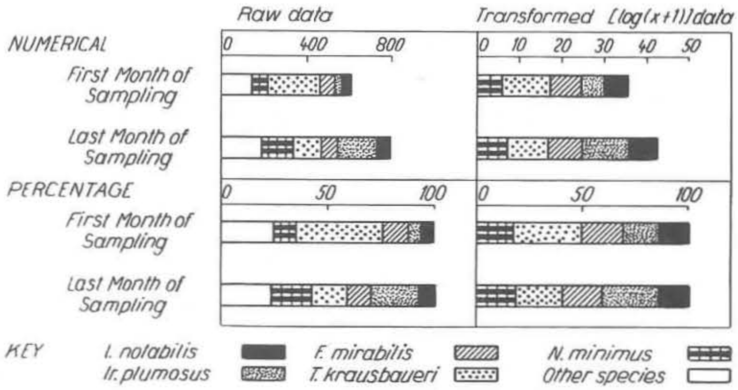


Fig. 5. Diagram illustrating the species composition of Plot A 4 for the first and last months of sampling for both raw and logarithmically transformed data.

Temperature:

The Ministry of Agriculture and Fisheries kindly allowed access to their records for the Bryn Adda N. A. A. S. Station which is 4 km. from Waen Wen. These records appear in Fig. 6 and show that, during the year, summer temperatures were abnormally low.

Sample moisture content:

The moisture contents of the three layers of the profile are illustrated in Fig. 6 and correspond with the rainfall figures. The moisture content of the litter is the most variable and both this and the humus layer had a maximum moisture content in mid-November, following the heavy rainfall of mid-October. The moisture content of the samples remained high throughout the summer of 1954 and this was probably due to the prolonged high rainfall.

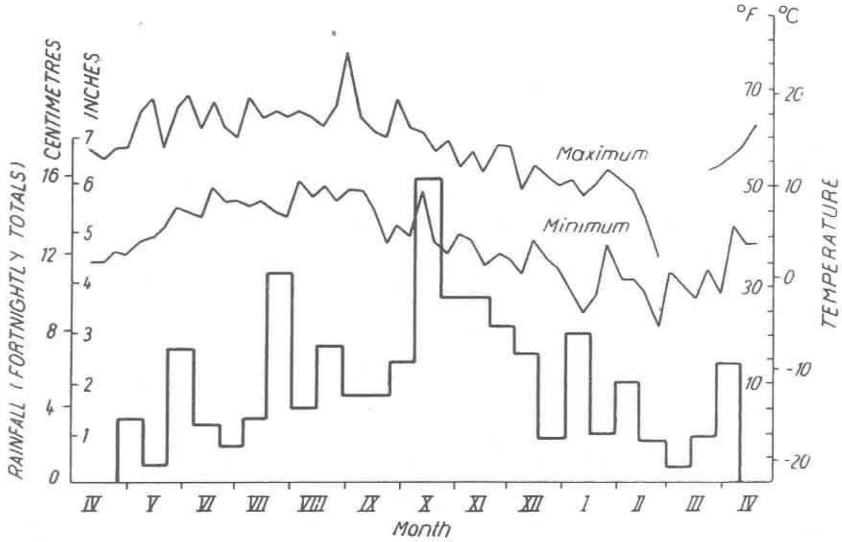


Fig. 6. Seasonal variations in rainfall and weekly maximum and minimum temperature records from April 1954 to April 1955.

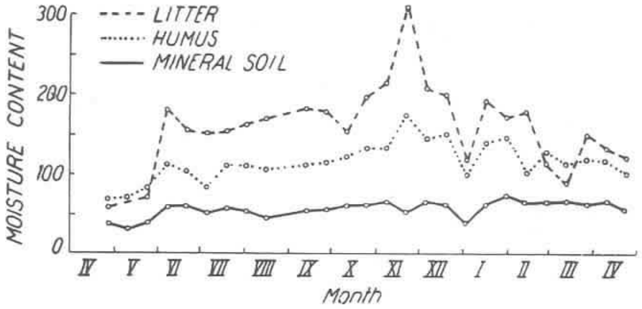


Fig. 7. Seasonal variations in the average moisture content of the samples from April 1954 to April 1955. (The moisture content is obtained by expressing the weight of water as a percentage of the dry weight).

3.23 Seasonal variation in collembolan numbers

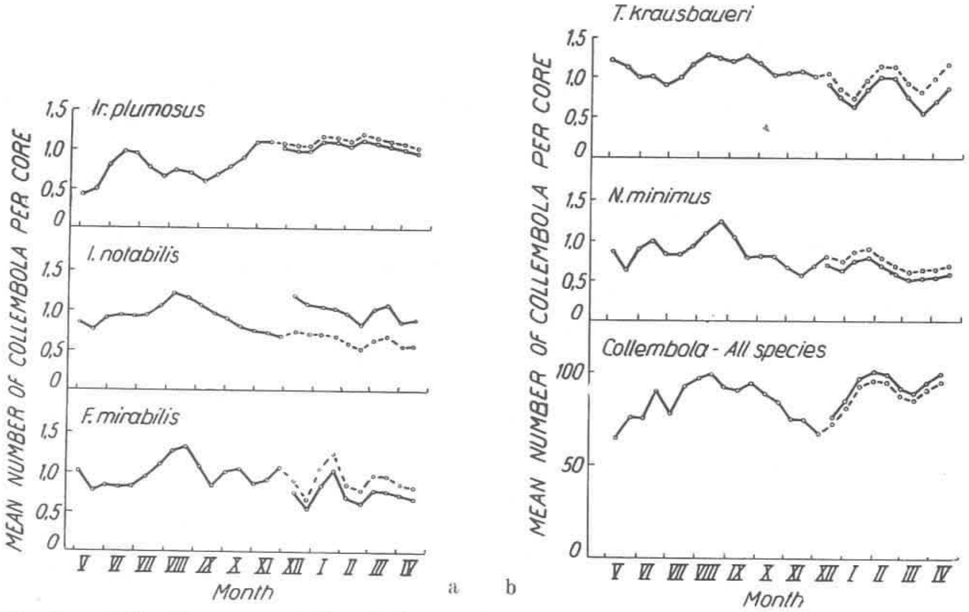
The fact that the collembolan populations are highly aggregated makes the sample totals based on twelve cores not too reliable an estimate of the true population. The conversion of the observations into logarithms minimises the effects of large aggregations and therefore gives numbers which are better estimates of the true size of the population; for this reason the logarithmically transformed data has been used in the preparation of the

graphs illustrated in Fig. 8 (with the exception of the 'total Collembola' figures which represent the running averages of three samples). Although these figures do not bear a direct relationship to the original collembolan figures, they give a more accurate picture of the population changes in the Collembola over the year. In addition to the use of transformed data the graphs have been smoothed by taking the running averages of two samples. In the cases of *I. notabilis*, *F. mirabilis* and *N. minimus* which are correlated with the depth of the organic layer, the figures have been corrected to a constant depth (= volume).

The collembolan populations after the gale damage have been corrected so as to be directly comparable throughout the whole year. The correction factor (C) was calculated as follows:

$$C = \frac{A}{A\,4a} \cdot \frac{A\,4b}{A\,4b + B}$$

where, A = Species total for Study area A (fortnights 1—16),
B = Species total for Study area B (fortnights 17—27),
A 4a = Species total for Plot A 4 (fortnights 1—16),
A 4b = Species total for Plot A 4 (fortnights 17—27).



Figs. 8a and 8b. Seasonal variations in the numbers of Collembola (Logarithmically transformed data has been used for the five commonest species. The observed data is represented by a continuous line and the corrected data by a broken line).

I. notabilis (see Fig. 8) had peak populations in August and these fell off steeply until mid-February which had the lowest recorded population during the year; after a very slight increase the population remained at a low level. First instar nymphs were found in the samples from May until early August during the build-up of the peak populations and did not occur again until early March 1955 when they were probably responsible for the subsequent very slight increase.

Ir. plumosus reached its maximum in June and this was followed by an August minimum; later it increased steadily until it reached a very high level in mid-October, remaining at this high level until the end of sampling in April 1955, when the population was double

that of the previous year. It seems, therefore, that conditions must have been very favourable for this species after its minimum of August 1954. A comparison between this species and *I. notabilis* shows that the population fluctuations for these species over the year had an inverse relationship.

F. mirabilis, *T. krausbaueri* and *N. minimus* all had an August peak and a small winter peak in January or February; they tended to decline after the summer peak but had small peaks at the beginning and end of the winter.

The figures for the total Collembola in the samples show peak populations in mid-August and early February; and minimum populations in early December. The figures for April 1955 are considerably higher than those of April 1954.

These results show that most species of Collembola had a large summer maximum and a smaller winter maximum in January or February. *Ir. plumosus* was exceptional in having a minimum in August and peaks in June and the winter months.

4 Discussion

4.1 Aggregations

It is well-known that few animals are randomly distributed throughout their habitat and Glasgow (1939) and Macfadyen (1952) and Haarløv (1960) have shown this is true of Collembola. The relative variance figures for the collembolan populations show that they are highly aggregated in Waen Wen plantation.

In the case of soil Collembola three possible explanations could account for the aggregations; they may not wander far from their original egg clusters (Murphy, P. W., 1955), they may be actively gregarious or they may be related to some patchily distributed environmental factor or factors.

The approximate numbers of eggs in an egg cluster have been counted in collembolan cultures and these figures make an interesting comparison with the figures for relative variance.

T. krausbaueri: No. of eggs/cluster 1—2 , relative variance 20.7—41.5
I. notabilis: No. of eggs/cluster 6—10, relative variance 21.5—38.2,
Ir. plumosus: No. of eggs/cluster 30—50, relative variance 8.0— 8.6.

Although the relative variance figures cannot be compared directly, being based on a single core size, these figures show that *T. krausbaueri* which has a highly aggregated population lays its eggs singly or in pairs. It therefore seems most likely that aggregations are not related to egg clusters.

It is possible that Collembola are actively gregarious; their habit of swarming on snow or water surfaces is well-known (see Davies 1932), although these may be exceptional circumstances. It seems unlikely, however, that active gregariousnesss alone can account for the aggregations in Waen Wen as the whole collembolan community is highly aggregated with a relative variance higher than those of the individual species populations. This implies that different species are aggregated in the same places, strongly suggesting that the position of an aggregation is determined by environmental factors. None of the measured physical factors showed variations of the same order as the collembolan populations and therefore aggregations cannot be accounted for on the basis of any single physical factor. Salt and Hollick (1946) and Neilsen (1954) could not account for the highly aggregated populations of wire-worms and Enchytraeidae, respectively, in the soil on this basis either. It seems possible that the aggregations are caused either by factors, perhaps biotic, which have not been recorded, or by the combined effect of several physical enivronmental factors, and it is reasonable to suppose that places where all these factors would be at an optimum would be patchily distributed. There is scope for carefully controlled laboratory work to investigate the preferences and behaviour of each species combined with work on a small area to study collembolan aggregations.

4.2 The relationship between Collembola and environmental factors

The results of the correlations show that the numbers of Collembola are influenced by the depth of the organic layer and its moisture content but the possibility of some other physical or biotic factor which is related to the depth and moisture content of the litter influencing the Collembola must not be ignored.

4.3 Variations in the numbers of Collembola in the plantation

The enforced change of study area during the year of sampling revealed some unaccountable variations in the wood. There were two known differences between the study areas; firstly, there were more trees in Study area A and secondly, the texture of the soil was more compact than in Study area B. The depth, weight and moisture content of the organic layers showed no consistent differences.

The faunistic differences were striking, the most obvious being the doubled numbers of *I. notabilis* in Study area B. It is possible that the loose-textured soil in this area was favourable to this species as it has been shown that although this species is not a true soil form it was capable of penetrating the mineral soil of this area. This means that in times of drought, *I. notabilis* can retreat into the deeper soil where it is protected from all but the most severe desiccation; this may act selectively in favour of this species.

The increased numbers of *I. notabilis* were offset by slight decreases in the numbers of the other common species, but the greatest decrease was in the numbers of 'Numerous' species in the second area. These species each constituted between one and five per cent of the total population. In Study area A there were eight of these species as against two in Study area B; it is possible that the numbers of these species had been reduced by competition from *I. notabilis*.

At this stage in our knowledge it is not possible to account for these differences in species composition for it is not even known why the particular species recorded were present in Waen Wen. There is little variation in the food and vertical distribution of the related species of similar size and it is difficult to picture twenty-three ecological niches each corresponding to a collembolan species. Possibly the whole collembolan community is in a constant state of flux with first one species increasing and then another, depending on the varied environmental factors favouring different species. Another difference between the two study areas was that the Collembola were much more patchily distributed in Study area B than in Study area A.

This comparison shows that, over a distance of 100 m., within a plantation which superficially appeared to be uniform, there can be marked differences in species composition. This implies that comparative surveys on a number of habitats are of limited value and until more intensive work is done on the structure of a collembolan community in a single area, few broad conclusions can be drawn regarding collembolan distribution, especially as the distribution of many species is very wide.

4.4 Vertical distribution of Collembola

The figures illustrating the variations between the vertical distribution of the different species of Collembola from Waen Wen show that each family has a characteristic vertical distribution.

It has long been realised that Collembola are morphologically adapted to a greater or lesser degree to either a subterranean or surface dwelling mode of life. This work has given numerical evidence of these ecological differences and shows that most species are intermediate in form between the two extremes, suggesting that they are adapted to an intermediate position in the profile. This agrees with HAARLØV's observations (1955) that the greatest numbers occur in the fermentation layer. There were no marked vertical migrations

of the five common species during the year of sampling and it is possible that this only occurs normally in times of drought, and was therefore prevented during this period by the high rainfall.

The study of the vertical distribution of Collembola in the deeper soil showed that the soil texture is probably important to Collembola as it may allow deep penetration of small hemi-edaphic species in times when the environmental conditions in the surface layers are unfavourable.

4.5 Variations in numbers during the year of sampling

Although it is impossible to draw general conclusions with regard to seasonal cycles from a single year's sampling, it is interesting to compare the times of maximum populations with the findings of other workers.

Most workers have found peak populations in the winter months, usually between November and February, and minimum populations in mid-August. The Waen Wen results show that four out of the five common species have a large August maximum and a smaller January peak. Some previous work has also shown an August maximum and STRENZKE (1949) found an August peak in semi-aquatic habitats for *I. notabilis* and *Friesea mirabilis*. GLASGOW (1939) found a slight peak in *T. krausbaueri* in August 1936 and VAN DER DRIFT (1951) found peaks in August 1936 for *Isotomiella minor* and Poduromorpha.

The usual cause of a summer minimum is almost certainly the dry conditions normal in many areas at this time of the year. The August peaks shown by STRENZKE's and the Waen Wen data lend support to this idea as both were from localities where moisture was unlikely to be a limiting factor.

The variations in the population of *I. notabilis* over the year of sampling show a general similarity in form to the temperature curve for the year, both having maxima in August and minima in February. It is possible that temperature was the controlling factor for this species during the period of sampling. An unexplained feature is the existence of a lower population in April 1955 than in April 1954.

A fact of considerable interest is that *Ir. plumosus* increased when *I. notabilis* decreased and vice versa. The population of *Ir. plumosus* in the spring of 1955 is double that of the spring of 1954, the result of a steady increase in numbers over the autumn and winter of 1954. This agrees with the observed distribution of this genus which tends to flourish in wet habitats. It is probable that the very wet conditions favoured this species at the expense of *I. notabilis*.

The species composition for Plot A 4 at the end of the year's sampling differed from that at the beginning. Apart from the differences already described for *I. notabilis* and *Ir. plumosus* there was an increase in numbers of *Folsomia 4-oculata* which in April 1955 would be included in the 'abundant' species grouping and slight decreases in *Tomocerus minor* and *Tullbergia krausbaueri*.

It is unlikely that the gale damage was itself responsible for the changes in species composition as the changes in numbers of, for example, *I. notabilis* and *Ir. plumosus* occurred simultaneously in both study areas and *Ir. plumosus* started its increase prior to the windfall. So little is known of the factors influencing the lives of Collembola that it difficult to account for population changes based on a single year's data.

5 Summary

The work described was carried out on a population of Collembola in a Douglas fir plantation in North Wales.

An average of 46,700 Collembola per sq. m. was recorded.

Samples of the collembolan population were taken at fortnightly intervals over a period of twelve months. These showed that the common species had a summer maximum and that the species composition differed at the end of sampling from that at the same time of the previous year.

The Collembola had aggregated populations and more than one species was agreggated in the same place.

Severe gale damage during the sampling year necessitated a change of the study area. A comparison of the two study areas revealed differences in species composition even though the centres of the two areas were within 100 m. of each other.

The numbers of three of the five commonest species in the soil core were shown to be related to the moisture content of its organic layer; three species were correlated with the depth of the organic layer.

An investigation of the vertical distribution of the Collembola in the soil profile showed that this was characteristic for each family and that Collembola were capable of penetrating more deeply the mineral soil when it was loose in texture.

5 Sommaire

Le travail décrit ici a porté sur une population de Collemboles dans une plantation de sapins Douglas dans le nord du Pays de Galles.

On a enregistré une moyenne de 46,700 Collemboles par mètre carré.

Les échantillons de population des Collemboles ont été relevés tous les quinze jours pendant une année. Ceux-ci ont révélé que les espèces ordinaires avaient des maxima en été et qu' à la fin de l'échantillonage la composition des espèces différait de celle qui avait été observée à la même époque l'année précédente.

Les Collemboles ont des populations agrégées et plusieurs espèces sont agrégées au même endroit.

Les dégâts causés par une forte tempête pendant l'année de l'échantillonage ont rendu nécessaire le changement de la région étudiée. Une comparaison des deux régions étudiées a fait ressortir des différences dans la composition spécifique bien que les centres des deux régions soient éloignés de moins de cent mètres.

On a constaté que l'importance numérique de trois des cinq espèces communes dans la parcelle de terrain était fonction de l'humidité de la couche organique; trois de ces espèces étaient en relation avec la profondeur de la couche organique.

L'étude de la distribution verticale des Collemboles par rapport au profil du terrain a montré qu'elle était caractéristique de chaque famille et que les Collemboles peuvent pénétrer d'autant plus profondément dans le terrain minéral que sa consistance est plus lâche.

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7 Appendix

Relation of the sampling dates to those of O'Connor (1957).

This work was done during the same period as that of O'Connor (1957) in the same habitat. The sampling dates were the same and cores were taken adjacently. The sampling dates were related as follows:

Fortnight 1 in this work = O'Connor's "Week 3"
Fortnight 2 in this work = O'Connor's "Week 5" etc.

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